Mechanical behaviour analyses of sap ascent in vascular plants

Jose-Luis Perez-Diaz · Juan-Carlos Garcia-Prada · Fernando Romera-Juarez · Efren Diez-Jimenez

Abstract A pure mechanical anisotropic model of a tree trunk has been developed based on the 3D finite element method. It simulates the microscopic structure of vessels in the trunk of a European beech (*Fagus sylvatica*) in order to study and analyse its mechanical behaviour with different configurations of pressures in the conduits of xylem and phloem. The dependence of the strains at the inner bark was studied when sap pressure changed. The comparison with previously published experimental data leads to the conclusion that a great tensile stress—or 'negative pressure'—must exist in the water column in order to achieve the measured strains if only the mechanical point of view is taken into account. Moreover, the model can help to design experiments where qualitatively knowing the strains and the purely mechanical behaviour of the tree is required.

Keywords Mechanics of a trunk · Finite element · Biomechanics · Sap pressure · Sap ascent · Strains in a trunk · Negative pressure · Cavitation · Water column stress

1 Introduction

There is no unresolved topic in plant physiology that had generated more literature than the anti-gravitational sap ascent in tall plants. This phenomenon has been studied from the times of Hales [1]. In the last four decades, most plant biology books assume the Tension–Cohesion Theory. The Tension–Cohesion Theory [2–5] proposes that the sap is pulled up through the xylem by water tension gradient generated by water transpiration at the leaves.

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This theory is extensively accepted in light of experimental evidence [6]. Nevertheless, many other physiologists reject it [7, 8]. It is hard to envisage how the xylem conduits can be treated simply as isolated pipelines. Moreover, the main problem of this theory is that very large negative tension must exist in the water column, which implies bringing the water up to very metastable states [9]. An alternative theory was proposed by Canny to explain this phenomenon, the so-called Compensating Pressure Theory [10]. In some cases, it is in great disaccord with the Tension–Cohesion Theory. Recent experimental techniques [11] claimed to show that considering plants as simple mechanical systems is a wrong approach and other points of view (osmotic, hydraulic, electrical, etc.) have to be included in order to completely describe their behaviour. This is why there is not any firm conclusion and it is still an open research topic. In order to design experiments to clarify, at least partially, this controversy, we have built a pure mechanical simplified finite element analysis (FEA) model of the xylem tissue of a tree. This FEA model is based on microscopic and macroscopic properties. Assuming the Tension–Cohesion Theory, the proposed model here relates the measurable strains of the tree with the mechanical interaction between the sap and the vessels.

The stem of a living tree is known to be continually suffering elastic changes in its diameter during the day, mainly because of sap ascent [12, 13]. It is commonly assumed that, according to the Tension–Cohesion Theory, periodic strains are induced in the trunk of the tree by the stress in the water column. From this viewpoint, it is assumed that the water column stress is directly transmitted to the vessel walls and it forces the whole trunk to contract. Other mechanisms like temperature, osmotic potential or secondary growth may also contribute to these diurnal strains [14]. Nevertheless, their contribution is assumed to be much smaller than that of the water column stress.

The phenomenon known as daily diameter changes or diurnal strains has long been studied [15–17, 27], relating different aspects of diurnal tree behaviours like water transport, sugar transport, wood morphogenesis or irrigation scheduling.

In this work, we focus on understanding the relationship between the stress in the water column inside the vessels and the diurnal strains. Several papers have showed that there are some elastic parameters that relate these strains with the water potential status [6, 18, 19]. Usually, these works propose some empirical methods for the determination of these parameters whose main disadvantages are that they cannot be applicable to different trees and that they are not constant during tree growth. Other kinds of related work try to establish general analytical models to predict mechanical tree behaviours from known water pressure status [20, 21]. Inversely, these last kinds of models would help to understand the water column pressure directly from strain measurements. It is accepted by the Tension–Cohesion Theory that sap ascent is due exclusively to transpiration-induced negative pressure gradients up to several megapascals through continuous water columns from the roots to the foliage. Water under such negative pressures is extremely unstable, particularly given the hydrophobicity of the inner xylem walls and sap composition. That is why determining estimated values for this pressure is so necessary.

We propose a pure mechanical 3D anisotropic model of a tree, based on the FEA. Its mechanical behaviour will be studied, admitting that there should be a tension or negative pressure on the xylem–water column interface. This is a consequence of the hypothetical negative pressure values of the water column, according to the Tension–Cohesion Theory. These interface tensions are traduced in measurable strains along the xylem and inner bark surfaces. The model makes it possible to calculate the tangential strains at the inner bark or at any point on the stem for different values of the water column stresses transmitted along

the sap/vessel interface to the walls of the conduits. Therefore, by measuring (for instance by extensometry) the strains at the xylem, phloem or bark, the tensile stress between the sap and the wall of the conduits can be derived. Moreover, it can be determined whether it follows the same pattern of daily changes as the internal pressure of the sap or whether it presents a limit that cannot be surpassed. In order to answer this question, only extreme values, not exact values, need to be estimated. The aim of this paper is not to provide an exact comparison of strains of any particular tree species, but rather an estimation of their magnitudes and extreme values in order to clarify the mechanical behaviour.

For the verification and comparison of the model results, some empirical data have been used. Particularly, this paper uses the experimental data found in the literature [22].

2 Model and method

We have modelled a European beech tree (*Fagus sylvatica* L.). It is an angiosperm with vessels, fibres and apotracheal xylem parenchyma, with uneven vessel distribution. However, in this model, vessels have been distributed evenly, with a diameter of 30 μm, with equal distances between each other. This assumption does not fundamentally alter the physical characteristics of the system, rather simplifies the calculation and is more likely to lead to a convergent result.

An elastic linear anisotropic behaviour of the European beech wood was assumed, and the values of the elastic constants given by the database of the Swiss Federal Research Institute of Zurich have been used [23]. *L* denotes the axial direction (parallel to the vessels), *R* denotes the radial direction (perpendicular to the rings) and *T* means tangent to the rings (Table 1).

The use of the macroscopic elastic properties for describing the microscopic properties is actually of limited benefit. The macroscopically uniform wood material is, in fact, composed of microscopic vessels and a complex material made by lignin, cellulose and other materials. We have done an extrapolation of the micrometric properties from the known microgeometry and the macrometric properties. In spite of the complexity of this material, its mechanical behaviour was approached as if it were constant and anisotropically known. In this sense, as the empty vessels do not contribute to the mechanical resistance, the macroscopic elastic constants will necessarily be smaller than the microscopic ones. By using the macroscopic constants as an approach for the microscopic ones, a lower limit for the elastic constants is used. This means that the real stems will be stiffer than those in this simulation, and therefore, real stresses may be larger than those calculated in this paper.

We have used the Algor® software to provide a FEA. It is a well-known method for solving partial differential equations, particularly elastomechanical equations [24, 25], which has a great number of applications and is extensively used in the fields of physics and engineering.

Table 1 Elastic anisotropic properties of the European beech

Young's modulus (MPa)	Poisson coefficients	Transversal elastic modulus (MPa)
$E_L = 14{,}000$	$\nu_{LR} = 0.450$	$G_{LR} = 1{,}640$
$E_R = 2{,}280$	$\nu_{LT} = 0.518$	$G_{LT} = 1{,}080$
$E_T = 1{,}160$	$\nu_{RT} = 0.708$	$G_{TR} = 465$

The method essentially reduces the continuous differential equations of an elastic problem to a (large) set of algebraic equations at certain nodes. These nodes are the vertices of the so-called finite elements. The elements are only the mathematical representation of the resistance tensor that transmits forces and displacement between nodes. The shape and size of the elements must usually be chosen carefully in order to get accurate results within a reasonable calculation time. In the case of our mechanical analyses, forces and pressures are set as external loads, and displacements are to be determined. For that, we can divide the whole tree into elements, but FEA requires a previous study in order to avoid unnecessary calculations. We have to take advantage of all problem symmetries, i.e. identical direction of displacements or inverse loads sets, as much as possible. Both hexahedral and tetrahedral solid elements were used, with a total of 5,000 nodes. By combining hexahedral and tetrahedral elements, the precision of the results was improved with a moderate number of nodes [24].

The trunk was assumed to be a perfect straight cylinder, axially symmetric, corresponding to a 1 m high stem with a trunk diameter of 10 mm. A transverse section was taken first, followed by a circular section. Then, only the circular section was modelled using the FEA program, corresponding to an angle of 1.2° which can be applied to the whole trunk (Fig. 1). This simplification is coherent with the symmetric properties of the problem which are implemented within the boundary conditions. The species and the size have been selected in order to fit the model to previously mentioned experimental data.

It was assumed that the core of the trunk (heartwood), with a diameter of 2.8 mm, has a much greater stiffness than that of the sapwood. Vessels were distributed, keeping their density between 100 and 200 units/mm^2—as observed in real stems. Although the average diameter of the vessels in an adult beech ranges from 50 to 90 μm, for a young stem, an average diameter of 30 μm has been estimated (Fig. 2).

As we can observe in Fig. 3, the above-cited circular section has been pierced by holes simulating the vessels. The section was divided into two zones, one containing the xylem

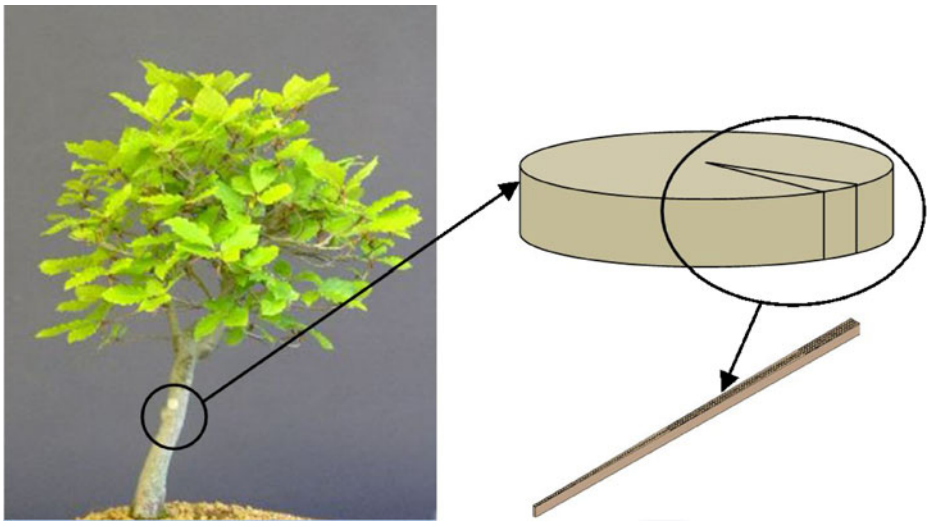

Fig. 1 Circular sector corresponding to an angle of 1.2° of European beech. The whole stem is completed by symmetry

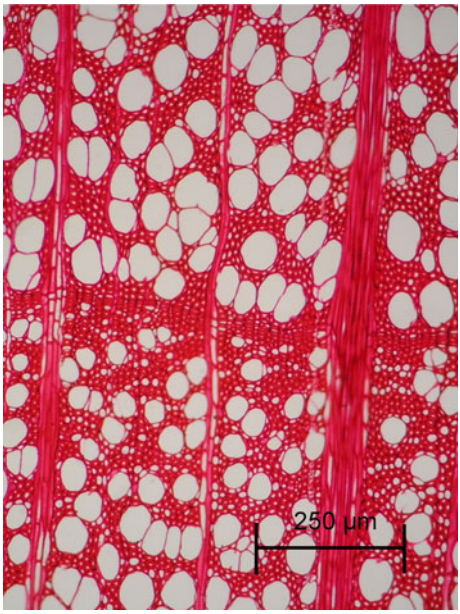

Fig. 2 Microscopic structure of the European beech (The Xylem Database - A web product of the Swiss Federal Research Institute WSL (http://www.wsl.ch/dendro/xylemdb/). Copyright: Fritz H. Schweingruber)

vessels and another the phloem. The choice of appropriate boundary conditions is key for obtaining coherent solutions to the problem. As mentioned, the core of the trunk was considered much stiffer than the xylem and the phloem and this condition was implemented with a restriction of all degrees of freedom, except for the axial displacements (*L*-direction). For the two rectangular surfaces delimiting the angular section, *T*-direction displacements were restricted. If we analyse the displacements of two hypothetical adjacent sections, we realise that the points of this surfaces only could move in the *R*- and *L*-directions. The *L* displacements are homogeneous over each *RT*-plane. Moreover, no torsion was assumed.[1] The outer cylindrical surface (inner bark) had an applied pressure of 0.101 MPa, corresponding to atmospheric pressure. The upper surface, perpendicular to the *L*-axis, had a pressure (0.108 MPa) equivalent to the weight of the upper part of the tree plus the atmospheric pressure. This is equivalent to the weight of half of the stem above. The lower surface had the reaction pressure to previous loads. Inside the vessels, both xylem and phloem, a pressure (negative or positive) was applied normal to the interface. Only these two last pressures (xylem water pressure, P_{XYLEM} and phloem water pressure, P_{PHLOEM}) have been changed. The rest of the boundary conditions and geometries have remained the same.

Two kinds of pressure variations were performed. The first aspect considered was the response of the finite element model of the trunk to changes in positive pressure, this pressure being the same at the xylem and phloem, ranging from 0 to 0.60 MPa. This simulated a pressure-imposed experiment like that of Alméras et al. [22]. Conversely, a negative pressure was assumed to be present in the xylem in a range between 0 and −1.00 MPa, with a positive (atmospheric constant) pressure present at the phloem. The

[1] The stems used in the experiments in this paper and the ones for comparison were not submitted to either torsion or strong wind loads.

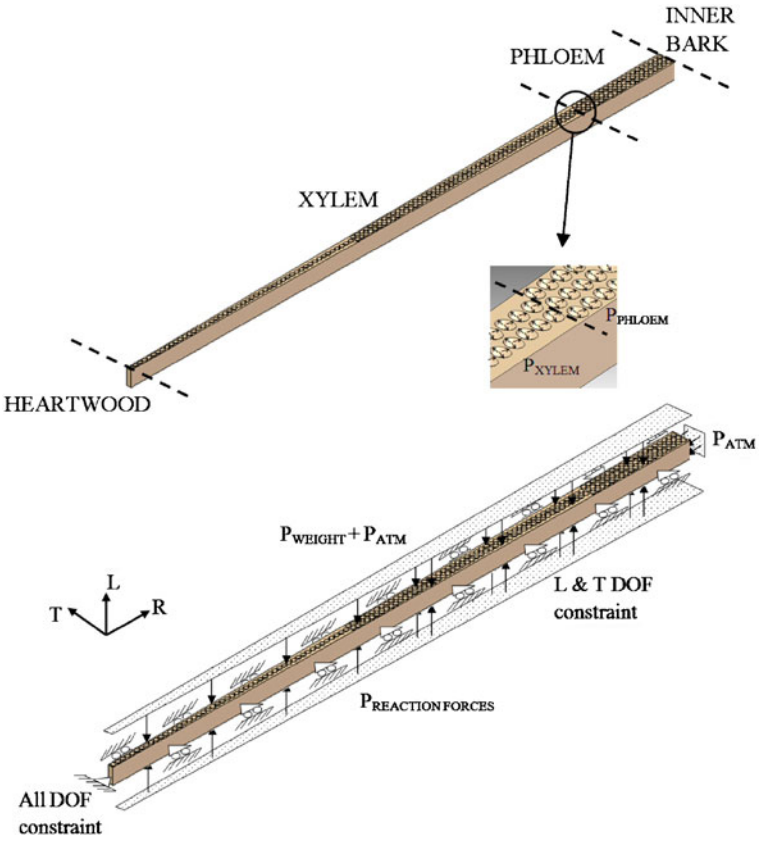

Fig. 3 Boundary conditions for the FEA tree model

range of values for the water column tension is in accordance with the Tension–Cohesion Theory for sap ascension [26]. In this model, it was assumed that this tensile stress is also applied on the walls of the vessels by negative water pressures. That means that a perfect adhesion in the interface is supposed and is not limited.

3 Results and discussion

Although the model permits measuring all strains at each node position of the circular section, only tangential strains have been recorded in order to compare with the experimental data.

The first part of the study (Fig. 4) shows the comparison of the tangent strains in the inner bark versus positive imposed pressure values. In the first configuration, when pressure is increased in both xylem and phloem vessels from the state of rest, we find a linear expansion of the model, producing an increase in the tangent strains. Despite having only a rough estimation of the elastic coefficients and the distribution of vessels, the values obtained for the tangential deformation are close to the experimental data obtained by Alméras cited above: for 0.6 MPa, we obtained a result of 779 μm/m at the inner bark.

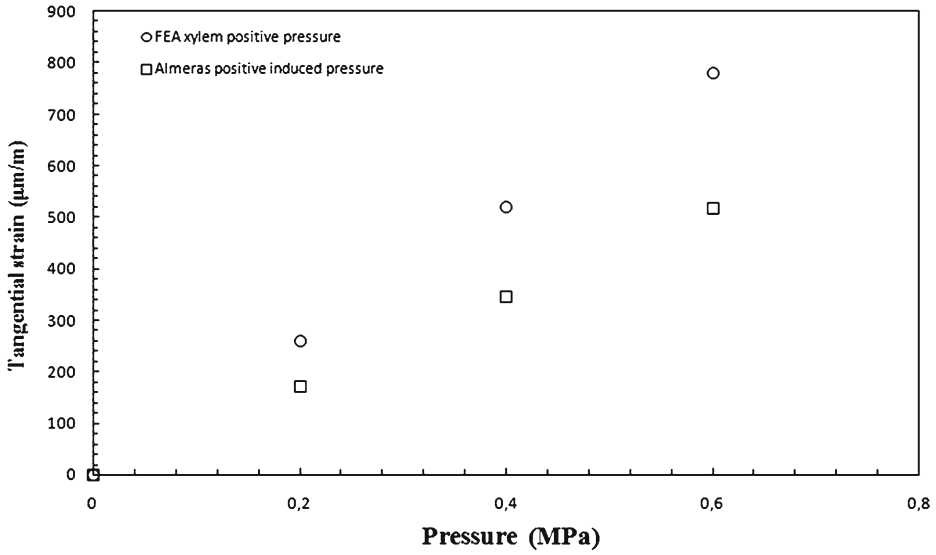

Fig. 4 Relation between tangential strains in the inner bark and imposed positive water pressures. Both model results and empirical data are shown

The cited experimental work by Alméras et al. gave 530 µm/m for the same position. We, to a certain degree, overestimate the sensitivity of the trunk of the stem to the pressure of the sap. Currently, the focus of this paper is not on getting a very accurate description of the microscopic elastic matrix of coefficients or an exact number or dimension of the vessels, but an overestimation of its sensitivity. We can then assure that the real sensitivity of the stems in the experiments will be lower than that in our model. From these results, we can conclude that our model is quite realistic. In the experiment [22], the stems were pressurised in a pressure chamber that involved the whole stem, which means that the xylem and phloem have the same pressurisation. Therefore, in our simulations, we have set as boundary conditions for the P_{XYLEM} and P_{PHLOEM} the same values.

Once we had checked the model, we performed the second part of the study, applying a negative pressure into the xylem ($P_{\mathrm{XYLEM}} < 0$), with a remaining $P_{\mathrm{PHLOEM}} = P_{\mathrm{ATM}}$. Thus, we have obtained new values of tangent strain; in this case, negative strains (contraction of the trunk) as expected. In this case, no measurements of negative tension were found for the case of our species. Nevertheless, on Alméras's paper, we found daily diameter changes. In Table 2, we show the extrapolated data taken from that paper.

In Fig. 5, we show the elastic response of the model to the negative pressure into the xylem. As we can see, the relation is totally linear. We have also added to the graph the equivalent pressure that the xylem should support for reaching the daily diameter changes amplitude of Table 2.

Table 2 Extrapolated data for the daily diameter changes under artificial light and dark conditions

	Amplitude of the change of tangential strains (µm/m)
Inner bark	637–740
Xylem	200–250

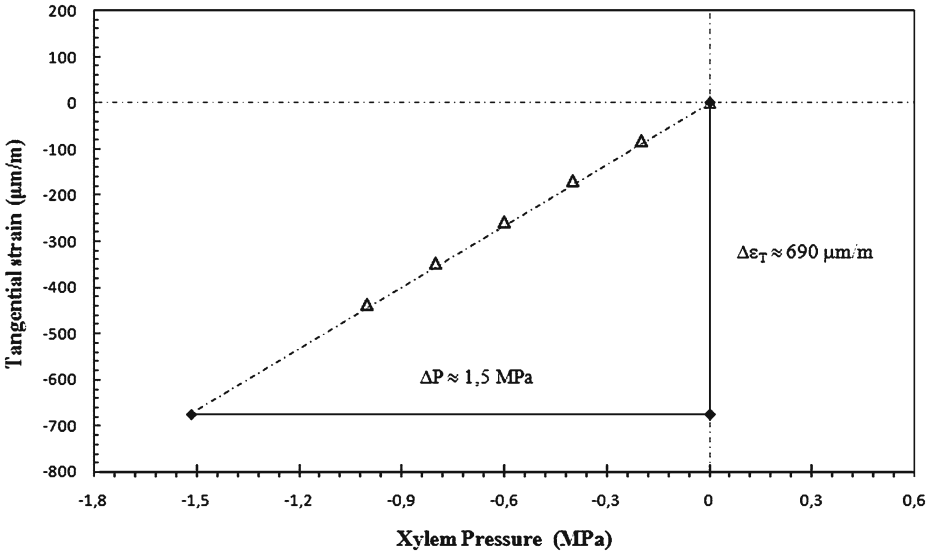

Fig. 5 Relation between tangential strains at the inner bark and negative water pressure into the xylem. Estimation of corresponding pressure for daily diameter changes

It is widely assumed that the sap pressure varies from +0.1 MPa to a negative value at the xylem sap. This makes the real value of the pressure changes greater than the estimation of 1.5 MPa. This means that the oscillation of the sap pressure at the xylem varies from +0.1 MPa to a pressure lower than −1.4 MPa (or a tensile stress >1.4 MPa). This negative pressure of −1.4 MPa must be transferred from the sap to the walls of the vessels in order to stress the wood and to produce the above-mentioned strains. In spite of our values not being interpreted as exact, they show the order of magnitude we are dealing with. This order of magnitude cannot be explained in terms of classical thermodynamics of fluids, which predicts cavitation to appear just at the vapour pressure of the liquid, on the order of +0.01 MPa [11]. The apparition of cavitation could be a problem with respect to the cohesion of the water column. This, therefore, demonstrates the existence of a real stress between the sap and the wood that completely surpasses any prediction or explanation of classical mechanics and thermodynamics of fluids.

Moreover, this model can be used to design further experiments in order to research the inner stresses and interactions among the different components of the living plants in a non-invasive manner. This model, as it is concluded from this paper, also considers the anisotropy of the stems as a key factor in the physics of vascular plants and can be a useful tool to clarify what remains unknown to date with regard to these important questions.

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